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Temperature and Embryonic Development in Relation to Spawning and Field Occurrence of Larvae of Three Antarctic Echinoderms

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Abstract. The effects of temperature on development and viability were measured at 14 levels between −2°C and +3°C on embryos of two asteroids (*Odontaster validus* and *Odontaster meridionalis*) and an echinoid (*Sterechinus neumayeri*) from Signy Island, Antarctica. Development rates were 2 to 10 times slower than those for temperate or tropical echinoderms, with times to hatching up to 240 h. Development rates for the two asteroids differed by 1.15 ×, and rates for both species approximately doubled over the experimental temperature range. In *O. validus*, embryo viability was independent of temperature, but in *O. meridionalis* viability declined with increasing temperature. Development rates for *S. neumayeri* were little affected by temperature above +0.2°C, but declined rapidly at lower temperatures. Conversely, the number of nonviable eggs was low and constant below +1.7°C, but rose rapidly at higher temperatures. A window of optimal temperature, between +0.2°C and +1.7°C, has therefore been proposed for development time and embryo viability in this population of *S. neumayeri*. Spawning trials and field observations of larvae indicated that the time of gamete release and periods of larval development in *S. neumayeri* coincided with austral summer sea temperatures in the same window. Embryos of *O. meridionalis* and *O. validus* are released in winter, when temperatures are constantly below −1.6°C. Comparison of the different strategies suggests that larval food supply and predation during planktonic phases are not the dominant ecological factors for these species.

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Introduction

Temperature and food availability are recognized as the two major factors affecting the development of marine invertebrate larvae (Thorson, 1950). The thermodynamic effect of temperature on physiological rates is a fundamental structuring element in biological processes and is perhaps the more straightforward of the two factors to understand. The powerful effect of temperature on larval development has long been recognized (Orton, 1920; reviewed by Pechenik, 1987). Nutrient availability, from reserves in brooded and lecithotrophic larvae and via feeding by planktotrophic larvae, is also clearly essential to sustain development to maturity. These factors should be of great importance in polar environments where temperatures are low and summer phytoplankton blooms short. However, the relative importance of temperature and resource availability to Antarctic larvae is not yet generally agreed upon (Clarke, 1992; Hoegh-Guldberg and Pearse, 1995).

The aim of this study was to investigate how the interaction of these two factors influences geographical distributions and reproductive strategies. Echinoderms were chosen because many of their Antarctic representatives have planktonic larvae (Bosch and Pearse, 1990). The three species used were the common cushion stars *Odontaster validus* Koehler and *Odontaster meridionalis* (Smith), and the regular urchin *Sterechinus neumayeri* (Meisner). All are ubiquitous and abundant in Antarctic waters, and their distributions overlap at Signy Island; all have been the subjects of previous research (McClintock *et al.*, 1988; Bosch and Pearse, 1990; Brey *et al.*, 1995). Both species of *Odontaster* have circum-antarctic distributions (McClintock *et al.*, 1988). *O. meridionalis* has a northerly limit at South Georgia (54°S, 36°W) and Ker-

guelen Island (49°S, 63°W), and occurs at depths between 15 and 590 m; whereas *O. validus* has been reported from Shag Rocks (53°S, 42°W) and Bouvetøya (54°S, 03°E), from 0 to 914 m (Clark, 1963). The obligate sponge-feeding *O. meridionalis* usually occurs at much lower densities than the predatory or scavenging *O. validus* (Dayton *et al.*, 1974). *S. neumayeri* is a nonspecific grazer (Pearse and Giese, 1966) and has a circum-antarctic distribution as far north as Kerguelen Island, from 0 to 400 m in depth (Brey and Gutt, 1991).

The larvae of both *Odontaster* and *Sterechinus* are pelagic and planktotrophic. Asteroid gastrulae develop into bipinnaria, whereas the echinoid gastrulae become plutei, both about 1 mm long (Bosch, 1989; Bosch *et al.*, 1987). *Odontaster* bipinnaria occur during the Antarctic winter, defined here as the mean period for which fast ice is present (Murphy *et al.*, 1995), usually under the sea-ice and at a time when very little phytoplankton is in the water column (Clarke and Leakey, 1996). The possibility of starvation in *O. validus* larvae has been investigated by Olson *et al.* (1987). Bacterivory has been proposed as a supplementary food source for asteroid larvae (Rivkin *et al.*, 1986), although its importance to Antarctic larvae has been questioned (Pearse *et al.*, 1991). However, the plutei of *S. neumayeri* develop and feed during the austral summer, a period of high phytoplankton standing crop and many associated zooplanktonic larval predators (Morgan, 1995). The larval phase of almost all marine invertebrates is the most vulnerable stage in their life history (Thorson, 1950). The ecological question is therefore, Why does such different seasonal timing occur in functionally similar echinoderm larvae from the same environment?

Materials and Methods

Spawning induction

Ten adults of each of the three species (*Odontaster validus*, *Odontaster meridionalis*, and *Sterechinus neumayeri*) were collected at monthly intervals by scuba divers in Borge Bay, Signy Island, Antarctica (60° 43′S, 45° 37′W). Collection depths and periods were as follows: *O. meridionalis*, 8–10 m from January 1994 to February 1995; *O. validus*, 36 m from February 1993 to February 1995; *S. neumayeri*, 16–18 m from February 1993 to February 1995. The animals were immediately transferred to a flow-through aquarium at the British Antarctic Survey research station for about 24 h, then put into 500-ml beakers of filtered (1.2 μm; Whatman GF/C) seawater standing in a shallow tank of running seawater. The gonadal regions of the starfish were injected with 1–2 ml of 1-methyl adenine (1MA, 10^{-4} *M* in seawater) (Chia and Walker, 1991), which induced spawning within a few hours if the animals were gravid (Bosch, 1989). To induce spawning in *S. neumayeri*, about 2 ml of 0.5 *M* KCl in seawater was injected into the coelom (Bosch *et al.*, 1987); gravid individuals spawned within a few hours of the injection.

Culture methods

An aluminium thermogradient block with apertures for 70 universal tubes (30-ml volume), in five rows of 14 tubes, was kept in a controlled temperature (CT) room set at +2°C. Thermocirculators at each end of the block were set at −2°C and +3°C respectively to represent the annual range of sea temperature around the Antarctic Peninsula and Sub-antarctic Islands (Foster, 1984). A 13-step temperature gradient was maintained with very low fluctuation. Construction notes and methods, with illustrations, are given by Baker (1974). The overall temperature range and variation at each step were monitored for 48 h before each experiment, and data were stored on a Grant Instruments "Squirrel" data logger. A precision electronic thermometer was used to measure the temperature of each culture prior to sampling. The culture water was exchanged every 48 h with precooled and aerated filtered (1.2 μm; Whatman GF/C) seawater. The five apertures at each temperature step were used as follows: two replicate larval cultures were maintained, and replacement water at the same temperature as the cultures was kept in adjacent apertures; the spare (fifth) tube was used for monitoring with the thermometer probe. The CT room was kept dark during the experimental period to minimize the possible conflicting effect of an artificial diurnal light pattern.

The development experiment was conducted on eggs and sperm collected at the peak of spawning for each species. These peak periods were different for each species, so the dates for the experiments varied accordingly: *O. meridionalis* embryos were incubated for 235 h starting on 22 July 1993; *O. validus*, 244 h starting on 15 June 1994; and *S. neumayeri*, 155 h starting on 17 October 1994. Eggs were collected in 1000-ml beakers and held in monolayers on the bottom of each beaker. Sperm were diluted with filtered seawater until translucent grey. To fertilize the eggs a few drops of the sperm were stirred into each beaker (following Strathmann, 1987). After a rapid wash in filtered seawater, the newly fertilized eggs were immediately transferred to the precooled universal (30-ml) vials in the thermogradient block. To prevent overcrowding, no more than a monolayer of embryos was put in the bottom of each vial (MacBride, 1900); this equated to about 250 embryos per incubation tube.

The remaining embryos were kept as controls in two 3000-ml beakers on a flow-through seawater table in the aquarium. A monolayer of eggs developed at ambient sea temperature and were stirred at the same time as the experimental cultures in the thermogradient block were

checked. Fertilization was confirmed after about 30 min by the presence of a fertilization membrane, as observed with a compound microscope at 400× magnification. The cultures at each temperature were observed alternately, to minimize disturbance (Bosch *et al.*, 1987).

Culture observation

Development in the cultures was monitored by pipetting about 100 embryos into a precooled cavity slide and photographing them at 12× magnification with a Wild M5 microscope, set up in the CT room. The cultures were observed every 4 h for the first 12 h, then every 12 h until the approach of hatching. When hatching was imminent, 4-h intervals were reinstated. The control cultures were observed at the same intervals and by the same method as the experimental cultures. Photographs were taken on Ektachrome ISO 200 transparency film, which was subsequently projected for calculating the various stages of development. The use of photography enabled development to be assessed rapidly, with minimal disturbance to the embryos. The times for 50% of the embryos to reach eight cells, blastulae, and hatching were recorded, together with the number of eggs and embryos failing to develop.

Data for each species were analyzed with Arrhenius plots (log of development rate as a function of the reciprocal of absolute temperature). Linear regressions were used where suitable, and compared using Minitab ver. 10 for regression analysis (Sokal and Rohlf, 1981). A broken stick model (one break) was fitted to *S. neumayeri* development times on the Arrhenius plot by the maximum likelihood method, using Genstat ver. 5.3 (Payne *et al.*, 1993).

Field observation of larvae

A two-year survey of the planktonic invertebrate larvae around Signy Island was carried out at the same time as the experiments described (Stanwell-Smith *et al.*, in press). Diver-towed nets and a handheld, diver-operated suction pump were used for regular sampling (method details in Stanwell-Smith *et al.*, 1997). Samples were collected at five sites at intervals of 2 to 4 weeks, both at 20 cm above the sea bed and 20 cm below the sea surface. A total of 317 net tows were made by divers. All relevant data were pooled to produce overall values of larval abundance in the water column.

Results

Development and embryo viability

The embryos were transparent, enabling easy identification of different development stages of each species. At the lowest incubation temperature (−2.02°C) the development times of *O. meridionalis* embryos were the longest, taking about 50 h for 50% of the embryos to reach the 8-cell stage, and 240 h for 50% to hatch (Fig. 1). A steady reduction in development time with increasing temperature was also observed. For all three species, times to hatching approximately halved over the experimental temperature range (−2.02°C to +2.83°C). In *O. meridionalis* the number of eggs remaining unfertilized had a strong positive correlation with temperature ($y = 2.59x + 11.15$, $r^2 = 0.95$. Fig. 2). Thus, the number of nonviable eggs increased with temperature from about 6% at −2.02°C to about 18% at +2.83°C; this was the reverse of the trend for development time. Development times for *O. validus* were similar to those of *O. meridionalis*, and the time to 50% hatching also shortened with increasing temperature (Fig. 1). However, in contrast to *O. meridionalis*, *O. validus* showed no relationship between temperature and its percentage of nonviable eggs ($y = -0.31x + 12.87$, $r^2 = 0.03$; Fig. 2), which averaged about 13%. The eggs that failed to fertilize constituted more than 95% of the embryos that did not hatch during the experimental period; the other 5% was composed of occasional embryos that divided only once or twice before ceasing development.

The time for *S. neumayeri* embryos to reach the 8-cell stage was between 15 and 40 h, and was similar to that for the starfish. Times declined by about half over the experimental temperature range, in a fashion similar to that seen in Figure 1 for hatching. The methods used here were unable to detect temperature-related differences in

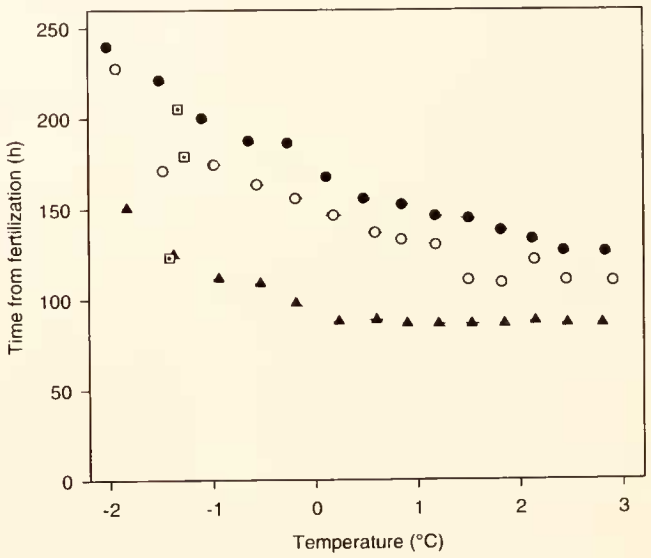

Figure 1. The time taken for 50% of *Odontaster meridionalis* (●), *O. validus* (○) and *Sterechinus neumayeri* (▲) embryos to hatch, as indicated by the loss of the fertilization envelope (Chia and Walker, 1991). Data were taken from photographs of larvae in cultures. The control cultures times are also indicated (⊡).

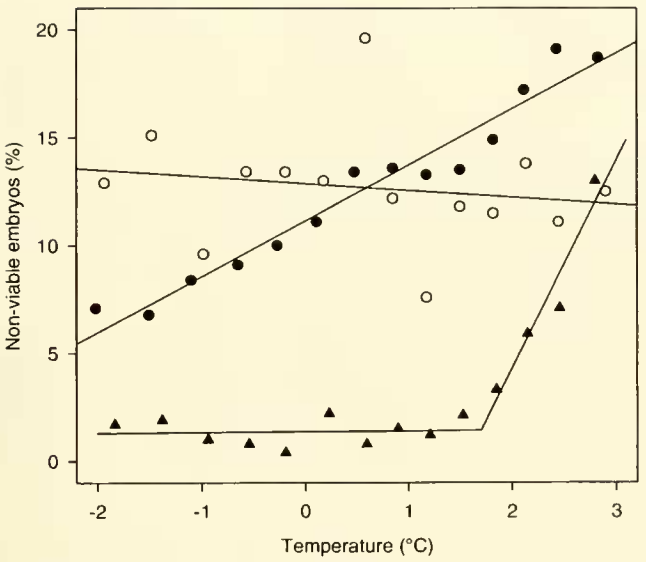

Figure 2. The number of nonviable eggs and embryos in each culture at each temperature step. *Odontaster meridionalis* (●) was fitted by linear regression ($y = 2.59x + 11.15$, $r^2 = 0.95$), as was *O. validus* (○) ($y = -0.31x + 12.87$, $r^2 = 0.03$). *Sterechinus neumayeri* (▲) data were fitted with a broken stick model by the maximum likelihood method (94% of variance accounted for).

development rates to the blastula stage for *S. neumayeri*, and results indicated that embryos took just over 40 h to reach this stage. Clearly, very small differences in development rate could have gone undetected. Data for 50% hatching times presented a different picture. Development time declined rapidly between −1.8°C (153 h) and +0.2°C (88 h). Above 0.2°C, times to hatching were independent of temperature. The percentage of nonviable eggs in *S. neumayeri* was very low and constant (about 1%) below +1.7°C (Fig. 2). Above 1.7°C, the proportion of nonviable eggs rose rapidly to about 13% at +2.83°C. A broken stick model (one break) fitted by the maximum likelihood method showed a break point at +1.7°C, and the fit accounted for 94% of the variance in the data.

Arrhenius plot

An Arrhenius plot is a simple description of the relationship between reaction rate and absolute temperature. Although originally developed for estimating activation free energies in enzyme kinetics, Arrhenius plots are often applied to the temperature behavior of complex biological systems (Clarke, 1983). When development rates based on the 50% hatch times (log transformed) for the three species were plotted against the reciprocal of absolute temperature (Fig. 3), data for both of the *Odontaster* species yielded straight-line relationships, and their slopes were not significantly different from one another ($F = 1.3$, df = 1, 24, $P = 0.27$). A common slope was calculated and fitted to the two data sets by analysis of covariance. The resulting intercepts were significantly different (difference = −0.0135, $t = -6.78$, $P < 0.0001$), indicating that *O. validus* embryos were, on average, developing at a rate 1.15 times faster than *O. meridionalis*.

A broken stick model was fitted to the data for the development rate of *S. neumayeri* (Fig. 3); the fit accounted for 98% of the variance. Maximum likelihood showed that the break point occurred at +0.2°C. Below this temperature, development rate increased rapidly with temperature ($y = 0.242x - 4.53$, $r^2 = 0.97$), but above it development rate did not alter significantly with temperature ($y = 0.006x - 4.47$, $r^2 = 0.23$).

Q_{10} *values*

The Q_{10} coefficient is a measure of the change in rate of a process with temperature (Cossins and Bowler, 1987). It is expressed as the factorial rate change over a 10°C temperature step and was originally devised for biochemical systems. It is useful here for comparing development rates between species and emphasising differences between rates. In physiological systems, Q_{10} values are usually between 2 and 3 (Clarke, 1983), and a Q_{10} of 1 indicates no change with temperature. Although the temperature range here is

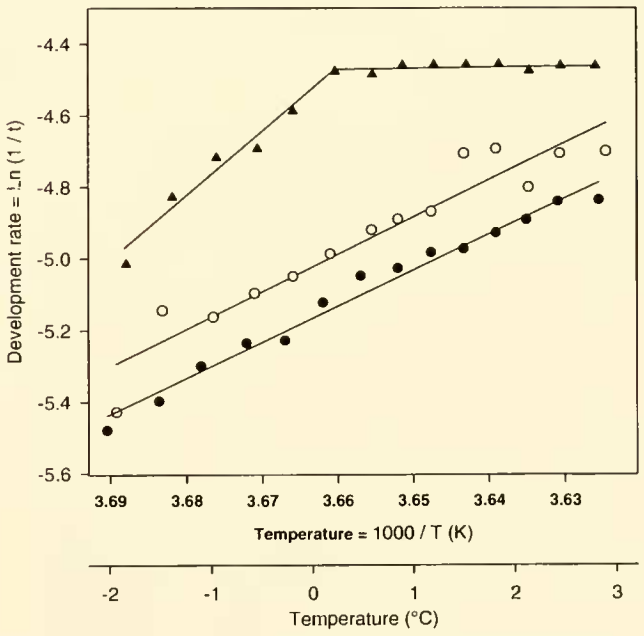

Figure 3. Arrhenius plot of the development rates of *Odontaster meriodonalis* (●), *O. validus* (○) and *Sterechinus neumayeri* (▲). Broken stick model fitted by the maximum likelihood method (98% of variance accounted for). Straight lines fitted by linear regression: *O. validus* ($y = 0.14x - 5.02$, $r^2 = 0.91$), *O. meriodonalis* ($y = 0.13x - 5.16$, $r^2 = 0.98$). Actual temperatures are also shown on second axis for clarity. Development rate was calculated as the reciprocal time to 50% hatching.

narrow (about −2.9°C to +2.0°C), the Q_{10} for development times to 50% hatching were calculated. Q_{10} = 3.8 for *O. meridionalis*, 4.5 for *O. validus*, and 13.6 below +0.2°C and 1.1 above +0.2°C for *S. neumayeri*.

Spawning and field observations

The results from the regular spawning trials were compared with environmental data from Clarke *et al.* (1988) and Clarke and Leakey (1996), particularly for sea temperature and microplankton chlorophyll *a* biomass for the period January 1993 to February 1995 at Signy Island (Fig. 4). Spawning was successfully induced in both the starfish species during the winter months (May—July). A few *S. neumayeri* individuals could be induced from June onward. Of these, only males spawned in June, July, and August; females could be induced from September onward. In both sexes, peak spawning induction occurred in November. Field observations of gastrulae have been combined with those for bipinnaria (for asteroids) or plutei (for echinoids) in the kite diagrams (Fig. 4), giving values for overall pelagic larval abundances in the water column. *Odontaster* larvae occurred between June and September of both years at densities up to 0.76 m^{-3}. *S. neumayeri* larvae were present between December and February in much lower numbers than the starfish (up to 0.09 m^{-3}), and were observed only during the 1993–1994 austral summer. It is clear that the timing of spawning

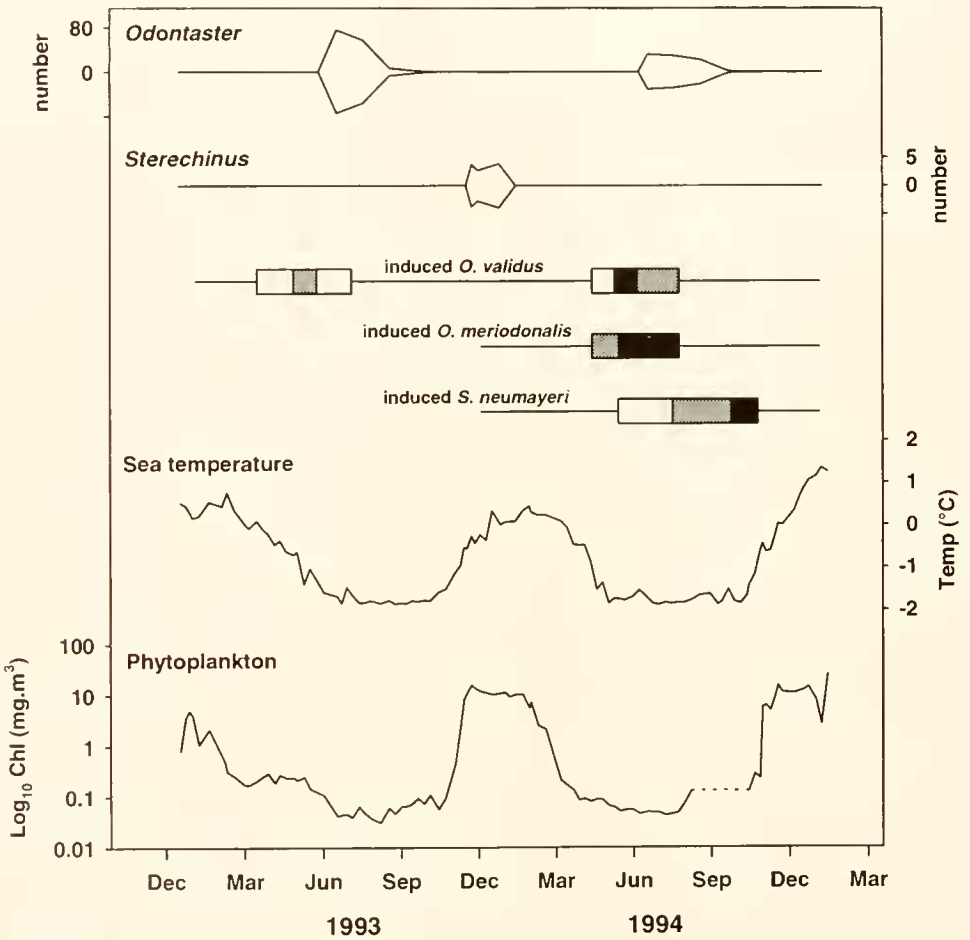

Figure 4. Field data collected between January 1993 and February 1995. The kite diagrams show the number of larvae caught (per 5000 l seawater filtered). The shaded bars show when spawning could be induced in the three echinoderm species: □ = 0%–25% animals spawned, ▨ = 25%–75% spawned, ■ = 75%–100% spawned. Note that the entire length of the lines indicate experimental duration (*Odontaster validus* was sampled for two years; *O. meriodonalis* and *Sterechinus neumayeri* were only sampled during the second year of the study). The chlorophyll *a* plot shows the microphytoplankton chlorophyll standing crop (>20 μm filter, mg · m^{-3}), with a dotted line indicating missing data. Temperature and chlorophyll data adapted from Clarke and Leakey (1996).

induction closely matches the observed seasonal pattern of larval occurrence in the wild.

Discussion

A reduction in development time with temperature (= increasing development rate) was observed in all three species (Fig. 1). This was expected, as development rates in Antarctic ectotherms are much lower than in temperate and tropical species (Clarke, 1992) and our data for *S. neumayeri* below 0.2°C agree with the general relationship found for echinoids (Fig. 5) from all latitudes by Bosch *et al.* (1987). Above 0.2°C the development rates depart from the general relationship. Development in *S. neumayeri* was 2 to 10 times slower than rates for temperate and tropical species at their normal habitat temperatures.

The changes in development rates with temperature of the two *Odontaster* species were not significantly different from one another, but *O. meridionalis* was 1.15 times slower at all measured temperatures (Fig. 3). Its slightly lower Q_{10} value may also indicate less influence of temperature on development rate. If temperature were the sole criterion, it would be advantageous for both species to release larvae in the warmer seas of the austral summer, when development would proceed at a rate about 1.5 times faster than in winter. However, other factors must be considered. The number of nonviable embryos released by the two species varied. For *O. meridionalis*, the number of fertilized eggs that did not develop further rose significantly as the temperature increased, from 7% at −2°C to 19% at +2.5°C (Fig. 2). For *O. validus*, however, the number of nonviable embryos did not increase with temperature, averaging about 12.5% throughout. This suggests that, for *O. meridionalis* at least, larvae gain some survival advantage by developing in the colder waters of winter.

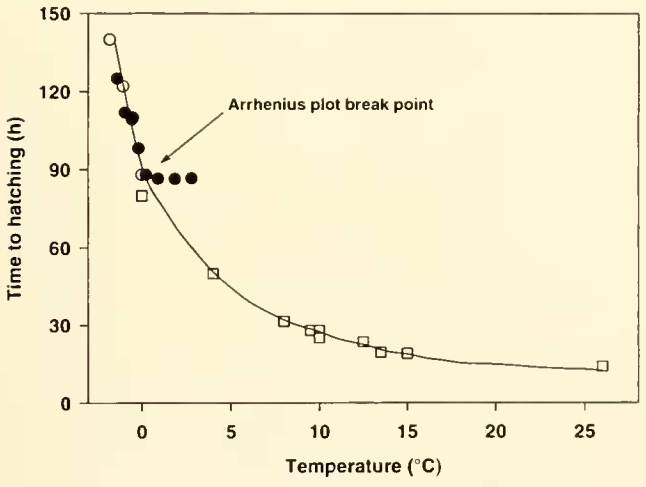

Figure 5. Duration of embryonic development to hatching as a function of temperature of several species of echinoids at different latitudes (adapted from Bosch *et al.*, 1987). Results from tropical and temperate species (□), *Sterechinus neumayeri* from McMurdo Sound (○), and *S. neumayeri* from the present study (●). The line was fitted by eye.

Looking at the field data (Fig. 4), it is clear that both *Odontaster* species spawn in the wild during the austral winter months and can be induced to spawn from May to August. As measured by Bosch (1989), the interval for *O. meriodonalis* and *O. validus* to develop from fertilized egg to feeding bipinnaria was about 35 days, which agrees with the timing of larval presence in the water column in the present study (June to September). These starfish probably obtain a reduction in mortality by avoiding pelagic predators associated with the summer phytoplankton bloom (Clarke, 1988). *O. meridionalis* also has reduced mortality at winter temperatures, as a result of the relationship between embryo viability and temperature (Fig. 2). The disadvantages of a winter spawning strategy include a slower (by a factor of 1.5) development rate and a diminished food supply. Slowed development rates may carry with them the extra energetic requirement of an increased overall maintenance metabolic cost when summed from fertilization to settlement (Clarke, 1992). It is possible that higher overall metabolic costs and reduced food availability are a disadvantage for winter larvae. However, Rivkin *et al.* (1986) produced evidence that asteroid larvae could feed on bacteria, and Peck (1993) found that larvae of the Antarctic nemertean *Parborlasia corrugatus* were capable of feeding on particles less that 1 μm in diameter. Bosch *et al.* (1991) showed that algae, bacteria, dissolved organic matter, and endogenous reserves could all make significant contributions to the nutrition of larvae of the Antarctic starfish *Porania antarctica*. In contrast, Pearse *et al.* (1991) found that bacterial ingestion by *O. validus* larvae was of little importance, and that temperate echinoderm larvae did not ingest bacteria at all. More recently still, Hoegh-Guldberg and Manahan (1995) and Prothero-Thomas (pers. comm) have found that metabolic rates are so low in Antarctic echinoderm larvae that they may not need to feed at all during development. Irrespective of these considerations, the wide distribution and abundance of *O. validus* and *O. meridionalis* demonstrate the success of their winter spawning strategy.

S. neumayeri has a different strategy. Below +0.2°C, its development rate was strongly influenced by temperature. The calculated Q_{10} of 13.6 is very high—beyond the range typically accepted as normal for biological systems (Clarke, 1983), suggesting that this response is not that usually presented by an enzyme-mediated reaction system. Other factors such as changes in membrane perme-

ability (Hochachka, 1991) may be important at temperatures at the lower end of a species tolerance range and, in the case of the Signy population of *S. neumayeri*, below +0.2°C. This would also suggest that below the break point for development rate data in the Arrhenius plot (Fig. 3), *S. neumayeri* is developing at the lower end of its range of temperature tolerance (Hoegh-Guldberg and Pearse, 1995). Above +0.2°C the development rate was independent of temperature up to the maximum temperature in the investigation (+2.8°C). The inference based on this observation is that development rate has reached its upper limit at 0.2°C, and further temperature rises are incapable of increasing the rate.

From temperature alone it would seem that *S. neumayeri* could maximize its rate of larval development by spawning when the sea was at or above +0.2°C, as in the austral spring/summer period at Signy Island. Once again the system is more complex than this. Embryo mortality in *S. neumayeri* is independent of temperature below +1.7°C, but increases rapidly above this: the next 1°C rise in temperature produces a 6-fold increase. The results (Figs. 2, 3) suggest there is a sea-temperature window between +0.2°C and +1.7°C in which development rate and embryo viability are optimized. The field data (Fig. 4) concur, showing that *S. neumayeri* produces embryos and larvae within the proposed temperature window. It is competent to spawn and can be induced to do so from May to October, when sea temperatures range between −1.8°C and −1.6°C. However, the period of maximum spawning competence was later than this, in November, when sea temperatures were approaching 0°C. (Such optimal temperature windows for development were also observed by Orton, 1920.)

Wild larvae were only found in the water column from about December to January, at temperatures around +0.5°C (Stanwell-Smith *et al.*, in press). Bosch *et al.* (1987) measured the development time from fertilization to plutei stage as about 20 days, suggesting the successful larvae seen in the water column had developed from gametes released in November, and that earlier spawnings in field populations are absent or rare. The rising sea temperatures observed in November may therefore be a cue for spawning in the Signy Island *S. neumayeri* population. The phytoplankton levels are also increasing at this time and have been closely correlated with spawning times in the patellid limpet *Nacella concinna* (Stanwell-Smith and Clarke, 1997), thus suggesting another possible cue (Starr *et al.*, 1990).

S. neumayeri larvae were also observed in plankton samples from McMurdo Sound during the end of November and the beginning of December (Bosch *et al.*, 1987), which was within the same interval that *S. neumayeri* larvae were observed in the present study (Fig. 4). The temperature at McMurdo remains constant at about −1.9°C (Littlepage, 1965), so this conflicts with the suggestion of optimizing a temperature "window." Spawning synchrony maximizes fertilization success in free-spawning animals (Levitan, 1995) and thus high-latitude populations would benefit from environmental spawning cues of some sort. Deep-sea echinoids exhibit aggregation prior to gamete release (Young *et al.*, 1992) as well as spawning synchrony. The thermal stability at McMurdo, as in the deep sea, suggests an alternative cue to temperature—perhaps phytoplankton?

Temperature and development were investigated in *O. validus* and *O. meridionalis* from populations at McMurdo Sound, Antarctica, by Hoegh-Guldberg and Pearse (1995). Their data show a different relationship than found for these same species at Signy Island, but are similar to the data for *S. neumayeri* (Fig. 3). Arrhenius plots of development rate were fitted with a broken stick model. The break point in the Hoegh-Guldberg and Pearse (1995) data occurred at 0°C, and the effect of temperature on development rate above that point was small. If the lower part of the broken plot were translated to the right in the Signy Island population, the break point for those embryos would be above +2.8°C. The plot for the Signy Island starfish would not, therefore, include a temperature range high enough to show a dramatic change in development rate. A translation of this type might be expected (Precht *et al.*, 1973) when going from a population adapted to the McMurdo marine environment, where temperatures are permanently about −1.9°C (Littlepage, 1965), to Signy Island, where the annual temperature ranges from a winter low at −1.8°C to a summer maximum between +0.5°C and +1.0°C (Clarke and Leakey, 1996). Applying the same logic to the McMurdo *S. neumayeri* data suggests that embryonic development rates in McMurdo populations of this urchin should have a break point at a lower temperature than that found in the present study (+0.2°C).

There are both advantages and disadvantages associated with the winter spawning strategy of the two starfish, *O. validus* and *O. meriodonalis*, and the summer spawning strategy of the urchin, *S. neumayeri*. However, neither the advantages nor the disadvantages are overwhelming. The data therefore suggest that the important selection criteria for these echinoderms are not associated with predation from bloom-associated predators or with the abundance of food. Other factors that could be important are egg quality, which should be related to previous adult nutrition, and predation by benthic suspension feeders during the settlement phase.

The relationships found here between development rate and temperature and between embryonic mortality and temperature may be important factors affecting distributions of Antarctic echinoderms. Variations in these characters between populations adapted to different tempera-

ture regimes clearly indicate their role in delineating the ability of a species to colonize a given habitat. The study also shows evidence for local population adaptation in embryonic development.

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